Early Journal Content on JSTOR, Free to Anyone in the World

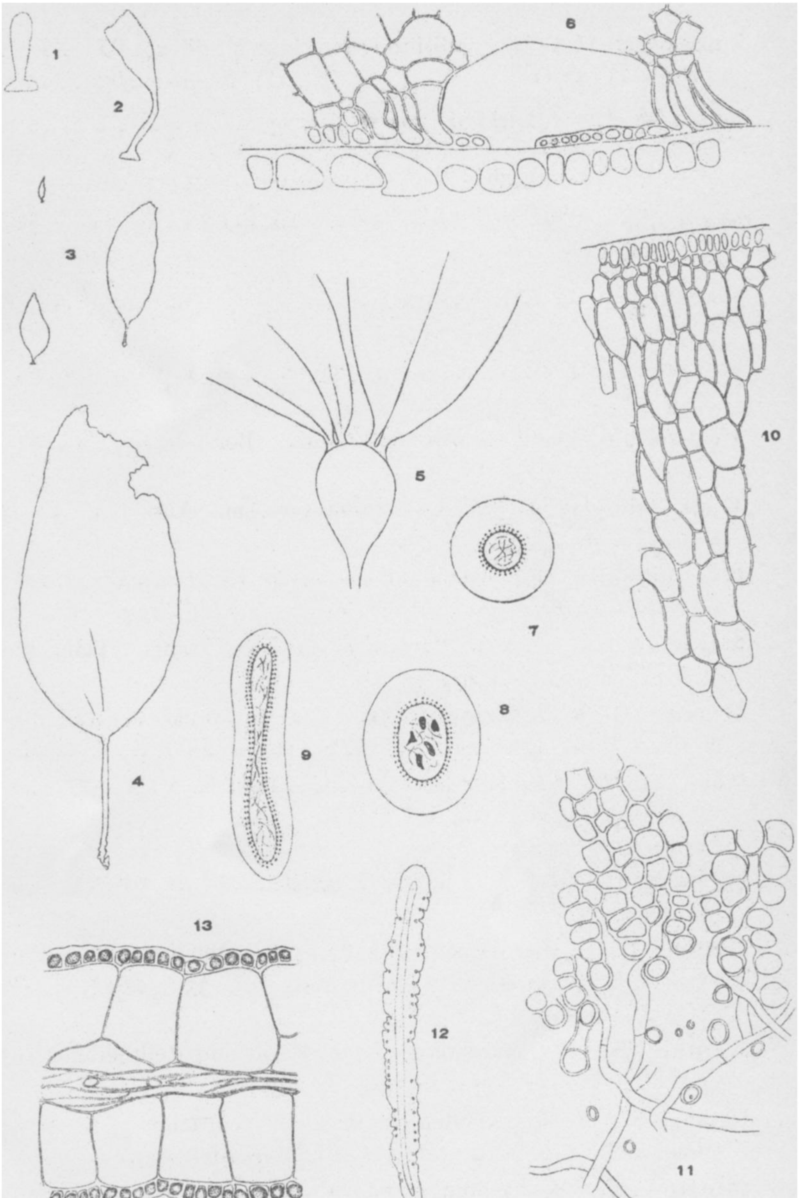
This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

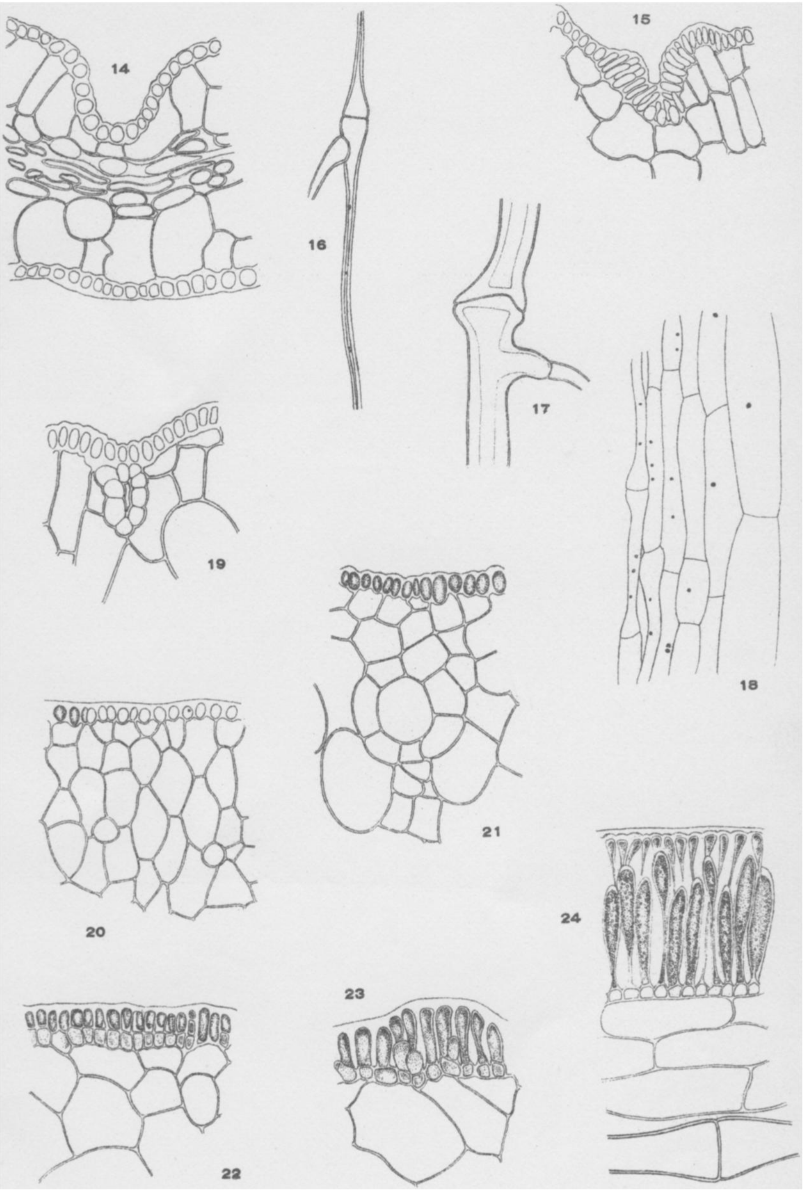
Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.



NEREOCYSTIS LÜTKEANA.

THE HELIOTYPE PRINTING CO., BOSTON



NEREOCYSTIS LÜTKEANA.

THE HELIOTYPE PRINTING CO., BOSTON

VOL. 29 No. 6

BULLETIN
OF THE
TORREY BOTANICAL CLUB

JUNE 1899

Observations on Nereocystis

BY CONWAY MACMILLAN

(WITH PLATES 361, 362)

Introductory and Historical.—The bladder-kelp of the northern Pacific coast, first described by Mertens in 1829 under the name of *Fucus Lütkeanus* and afterwards made the type of the genus *Nereocystis* by Postels and Ruprecht, has never received the study that its great size and abundance would have led one to expect. A brief and incomplete account of its anatomy is given by Postels and Ruprecht in their *Illustrationes Algarum*, in which Plate XXXIX., Figs. 24–30 are of the histology of the mature stipe, pneumatocyst and lamina. The most extended anatomical study is that by Oliver in his paper on the *Obliteration of the sieve-tubes in Laminariaceae*, published eleven years ago in the *Annals of Botany*, while some isolated references may be found scattered through the literature of the Laminariaceae and that of West American algae.

I have had the unusual opportunity of examining some hundreds of specimens of *Nereocystis Lütkeana* collected at Puget Sound during 1897 and 1898 by Miss Josephine E. Tilden. The series includes undoubted specimens from one-half of a millimeter in length to eighty feet and serves to illustrate many points of the anatomy and development which have not hitherto been described. Still younger forms carrying the series back close to the germinating spore are probably in the collection but I am not yet prepared

[Issued June 17]

to speak with absolute certainty of any plant under one-half millimeter in length. The reason for this is that the youngest plants, collected in two feet of water off San Juan Island at 10 A. M., June 5, 1898, during the lowest low tide of the year, are mingled with young *Costaria Mertensii*, *Laminaria saccharina* and *Alaria*. It is difficult to distinguish the young stages of Laminariaceae from each other and this difficulty increases inversely with the age of specimens. Yet a careful comparison of sections shows structural peculiarities which enable one to speak with some degree of certainty.

The first published reference to young *Nereocystis* plants and the first descriptions of their fruiting structures are those of Areschoug in a paper in the Swedish journal, Bot. Notiser of 1876, pp. 65–73 and in Observationes Phycologicae. In the first paper Areschoug describes his *Pelagophycus giganteus* under the name of *Nereocystis gigantea*. In this article he describes the young unilaminate plant and explains how the lamina is split vertically and how each half is repeatedly split. He describes the change in shape of the pneumatocyst as it develops and makes some anatomical observations upon the mucilage ducts which are quoted later by Guignard. The resemblance of the young *Nereocystis* plant to young *Laminariae* was apparent to him.

The only previous American reference that I have found to young *Nereocystis* plants—in which, I have been unable to discover any addition to the facts set down by Areschoug thirteen years before—is in one of the more recent papers of Professor W. G. Farlow of Harvard University who, in the BULLETIN of the Torrey Botanical Club for 1889, comments upon a series of young plants presented to him by Miss Lennebacker, concerning which, however, I have not learned that he ever published further. The smallest plant he mentions was four inches in length and he states that the "bladders begin to show themselves when the plants are about eight inches long." It is possible, however, by the sense of touch to distinguish the pneumatocyst in material but three centimeters in length and the organ becomes visible as a slight expansion of the stipe shortly after. Professor Farlow, with Areschoug, observed the resemblance of the immature plants to young Laminariaceae of the digitate section, possibly basing his statement upon Foslie's plates. It is certainly striking and even more so when still younger material is compared. I do not know what precautions Miss Lennebacker took in the selection of her series, but from Professor Farlow's observation that the stipe is slender and *short* I should think that possibly some *Laminaria* sporelings might have been included. My own researches have shown that in *Nereocystis* plants only one millimeter in length the stipe is nearly as long as the lamina while in plants three centimeters long the stipe is five millimeters in length, showing an early, rapid elongation of the lamina.

General Structure.—The general organography of *Nereocystis* may be best explained by describing the plant as made up of two principal areas—a proximal, affixed portion and a distal free portion. At first when the plants are merely elongated pear-shaped bodies less than .1 mm. in length (as probable from the examination of material that I am yet compelled to consider doubtful) the holdfast or proximal portion is spread out as a disc-shaped foot from the under side of which numerous rhizoid-protuberances are affixed to the substratum, while the distal portion enlarging apically is still of a generally cylindrical shape. This primitive holdfast or "primitive disc" recalls the similar structure described for young specimens of *Saccorhiza dermatodea* by Professor Setchell and for *Laminaria* by Foslie. As in *Saccorhiza* the primitive disc is provided with a crenate margin which becomes lobed and the lobes develop into protuberances which may be termed the primitive hapteres. Later when the plant is a centimeter or more in height, but sometimes not until four or five times as long, the secondary hapteres begin to show themselves as rows of emergences just above the point where the primitive disc passes over into the distal portion of the plant. These secondary marginal hapteres flatten themselves where they come in contact with the substratum and the whole primitive disc develops into a sucker-shaped cup. Above the first secondary hapteres others commonly develop, the number of emergences in the broken whorls being somewhat variable, but in general each emergence stands over an emergence of the whorl below. In this way, finally, a large hapteric area, the "holdfast," is developed consisting of hundreds of dichotomously branched cylinders and forming a ramose body more than a foot in diameter.

The primitive disc finally stands near the center of the great fixation-organ made up of the hapteres progressively developed from above. If growing upon a flat surface, the ends of the hapteres originating from higher whorls on the stipe stand concentrically outside of those belonging to hapteres of lower whorls and the whole apparatus is to be diagrammed as a series of superposed cones very much flattened and split.

In old material of *Nereocystis* a great many confluent callosities may occur along the stipe. These originate from emergences precisely similar to those which produce hapteric branches and probably the callosities may be regarded as homologous with unattached hapteres. I have not observed dichotomy in any of the callosities nor need I discuss at length their probable function. It suffices to indicate their great similarity of origin to the secondary hapteres, suggesting that the whole stipe is capable of forming holdfast organs from the base to the pneumatocyst. The callosities are sometimes as large as one's finger and spirally disposed around the slender stipe reminding one a very little of a loose growth of *Cuscuta* on the stem of a flowering plant. This position I regard as indicating torsions of growth in the stipe and it has been clearly observed that while the elongated callosities are in some cases confluences, in others they originate from single original hemispherical protuberances. On the stems of young plants a foot or two in length the callosities are extremely rare, but they progressively develop and increase in number and size until old stems are abundantly provided with them along much of their extent. They are particularly in evidence when two or more plants growing close together have twined about each other as they often do. On the stipes of such the callosities are developed as a continuous cushion where the stems are in contact. Although really organs of the stipe, I have mentioned these callosities at this point because of their evident homology with the hapteres.

The distal end of the *Nereocystis* plant finally differentiates itself into three areas, stipe, pneumatocyst and lamina. When very young no distinction between these areas is visible, but in the smallest plants I have seen—and they may possibly be *Costária*, *Laminaria* or *Alaria* sporelings rather than those of *Nereocystis*—the stipe is marked off by a sharp constriction from the primitive disc and gradually enlarges distally into a portion which afterwards undergoes a lateral flattening into lamina. The pneumatocyst originates as a swelling in the stipe just below the lamina and is the last of the three distal members to come into existence as such. At first the lamina is single and uncleft, of a rather narrow, lanceolate shape and becoming narrowly ovate with acute tip as it grows older. The first longitudinal slit which separates the lamina into two halves right and left appears near the base of the lamina (according to my series of young forms) when the length of the whole plant has reached about 13 cm. This cleft is the only one which reaches clear to the surface of the pneumatocyst though the second cleft comes very close and divides the two laminae into four. Oliver's statement, no doubt based upon an incorrect figure of Postels and Ruprecht, that as a rule five petioles are borne upon the pneumatocyst is quite unconfirmed by any of the plants which I have examined. On the contrary as pointed out by Areschoug there are but two main distinct laminae each of which is cleft almost to the base by the secondary longitudinal furrows and tertiary and successive furrows cleave these laminae almost to the base, so that a hasty examination suggests the presence of two tufts of leaves. In each tuft there may be twenty-five or more lobes or leaves. The resemblance of the leaf arrangement to that in Areschoug's *Pelagophycus giganteus*, a plant of the Californian coast and by some American students still maintained to be congeneric with *Nereocystis Lütkeana*, is certainly very demonstrable.

The origin of the clefts and of the pneumatocyst is better discussed in the histological portion of my paper but the primitive differentiation of lamina and stipe, since it arises simply by the lateral flattening of a primitive piriform distal bulb, may be noted here. At first the lamina is shorter than the stipe but after the plant has become about a tenth of a millimeter in length the lamina begins to elongate relatively faster for a time, but when the plant has reached a length of twelve or thirteen centimeters the elongation of the stipe becomes relatively more rapid and this ratio continues so that in a plant eighty feet long the stipe measures forty feet, from hapteres to pneumatocyst, and another forty to the tips of the slender ribbon-shaped lobes of the two great leaves. But in longer plants the stipe is proportionately more extended while the leaves rarely come to exceed fifty feet in length. This measurement of the leaves much exceeds that given by Mertens in his letter to his father published by von Chamisso in the 1829 volume of Linnaea. Mertens gives twenty-seven feet as the extreme leaf-length and Oliver, quoting no doubt from this original account by the discoverer places the leaf-length at eight meters. We have, however, leaves nearer fifteen meters in length than eight. A hundred meters as the extreme length of a mature individual, the figures given by Kjellman in the Engler-Prantl Natürpflanzenfamilien, is not at all excessive. Of this at least eighty meters would belong to the stipe, two or three meters to the elongated retort-shaped pneumatocyst and the remainder to the laminae.

The breadth of mature lobes of the lamina is from 8 to 12 cm., the diameter of the stipe is from 8 mm. to 2 cm. just under the pneumatocyst area, the pneumatocyst is sometimes 15 centimeters in diameter just below the attachment of the lamina and the branches of the haptere-cluster range from 3–5 millimeters in diameter. These measurements are all conservative and larger individuals may no doubt be found.

When first formed the pneumatocyst is spherical and retains this shape in plants 30 cm. long. Later it becomes ovoid and then piriform. In a plant 30 cm. long the pneumatocyst is one centimeter in diameter. In a plant 50 cm. long the pneumatocyst is 2.5 cm. in diameter and 3 cm. in length. After the plant has attained a length of 3 or 4 meters the pneumatocyst begins to elongate and from that stage until maturity maintains the characteristic retort-shaped appearance finally becoming 2 or even 3 meters in length, in which condition, as long ago noted by Mertens, it is employed by the Aleutians to siphon water from their canoes. By the same tribes, Mertens also observed that the stipe is employed for fishing lines. As learned by Miss Tilden such lines are still preserved as curiosities by a few native fisherwomen, but ordinary tackle is generally in use.

Reproductive Area.—The only functional reproductive bodies known to occur in *Nereocystis* are the spores, formed in sporangia. Together with the paraphyses these sporangia produce large soral patches on both sides of the leaf. A sorus may be as much as a meter in length, from 3–7 cm. in width, and on a single leaf three or four such sori may occur, their ends separated by but a few centimeters of sterile tissue. The leaves which bear the sori are rather broader than the sterile leaves. Fruiting patches are very conspicuous on account of their slightly lighter color than the sterile tissues. Oliver writing in 1887 states categorically that nothing is known of the reproduction of *Nereocystis*, but Areschoug in 1876 observed the sporangia and paraphyses together with some young forms, as indicated in his paper in Bot. Notiser, and afterwards in 1884 returned to the subject in his *Observationes Phycologicae* where a brief systematic description is given. My own researches have cleared up the origin of the sporangia and paraphyses and I have been able to follow the development of the sorus from its first inception.

Ecology.—The habit of mature *Nereocystis* plants is to attach themselves in channels where the tides are swift and beds of the plant are to be looked for in tide-ways. I think that plants which are adapted to life in strong tide-ways and tide-rips should be distinguished as a special ecological sub-class of hydrophytes distinct from such plants as *Fontinalis* which grow in river-channels and may be termed *rheophytes.* Previously I have noted the adaptation of certain limnetic plants to withstand the impact of surf and proposed for them the name of *cumaphytes.* I now venture to suggest that plants like *Nereocystis* or *Alaria* be regarded as typical of the tide-way habitat and be known as *palirheophytes.* When the tide is not running the pneumatocysts float more nearly perpendicular and show as round bulbs at the surface of the sea, but when the tide begins to run tension is exerted on the stipe and holdfast and the long retort-shaped pneumatocysts lie lengthwise with the current. The leaves are always somewhat submerged; especially is this true when the tide is running—a habit which protects their more delicate bodies from the destructive friction and impact of the surface. When the tide changes the shifting of the great pneumatocysts is sufficient in force to overturn small skiffs which may be caught among them. But larger boats find a *Nereocystis* bed a safe anchorage if a storm overtakes them while near the rocks of a leeshore, and Puget Sound fishermen often anchor their boats to a dozen of the *Nereocystis* pneumatocysts and have no fear of being blown upon the rocks, so firmly are the hapteres attached to the bottom and so strong are the stipes. In the late autumn the *Nereocystis* dies, for, as long ago noted by Mertens, while one of the largest of the algae it is an annual.

Histology.—The intimate structure of the Laminariaceae has commanded the attention of many careful observers. Among the more important papers that I have consulted may be mentioned those of Postels and Ruprecht (1840), Ruprecht (1848), Thuret (1850), Le Jolis (1855), Agardh (1868 and 1873), Reinke (1875), Janczewski (1875), Areschoug (1876), Foslie (1884), Will (1884), Wille (1885, 1897), Kjellman (1883, 1893), Grabendörfer (1885), Oliver (1887), Rosenthal (1890), Setchell (1891), Guignard (1892), Murray (1893). Few of these make any mention of *Nereocystis*, but since in details of structure the genera of the Laminariaceae are rather similar, all these papers and several others have been of assistance.

In general, as particularly demonstrated by Reinke and Wille, the Laminariaceae have well-marked tissue-areas which may be regarded as in a degree physiologically equivalent to those of higher plants. Cortex and central cylinder are distinguishable in stipes and laminae. Mestome, stereome, tegumentary and photosynthetic areas are well differentiated although the second, to which Setchell's sclerenchyma of *Saccorhiza* may belong, is poorly developed as in most hydrophytes.

The primitive Disc.—Longitudinal sections of a primitive disc belonging to a plant 18 mm. in length showed it to be irregularly circular in shape, .8 mm. in diameter, .1 mm. high. Near the center of the upper side arises the stipe with a diameter of 75 mic. The primitive disc consists of parenchymatous tissue of approximately isodiametrical polyedral thin-walled cells about 12 mic. in diameter. The superficial layer is made up of much smaller epidermal cells similar to those which occur over the stipe and lamina. The layer of cells which is appressed to the substratum—in this case the surface of a *Zostera* leaf—are for the most part similar in shape to the general fundamental tissue of the disc but not much more than half as large. Some of these appressed cells are prolonged into stocking-shaped rhizoids the flat surfaces of which lie very close against the epidermis of the eel-grass. Measurements of some of these stocking-cells showed them to be 7 mic. in diameter, the leg and foot of the stocking each being 15 mic. in length. Just above the area of affixation numerous transverse partitions are visible in the fundamental tissue of the disc and apparently there is here a layer somewhat similar to the cambial zone of higher plants and by it the primitive disc becomes thicker. At the same time divisions in various planes cross the more internal cells of the fundamental tissue and the epidermal cells increase in number by vertical divisions. As elsewhere in the plant the epidermal layer of the primitive disc is abundantly provided with chromatophores, which in my aniline-water-safranin preparations are stained deeply, while the fundamental tissue cells are given a pink hue by the staining of their thin walls. At this age the margin of the primitive disc has not yet become crenate, although the slight irregularities of its circular form will in older material bring about the crenations of the margin which eventually protrude themselves as the primitive hapteres. While the primitive disc is in the condition just described, the medulla of the stipe is sharply distinguished from the cortex by its longer and narrower cells, but the differentiation of sieve-tubes and pith-web has not yet taken place. Rather is the whole area of the stipe made up of prosenchymatous prismatic cells without intercellular spaces and the cortex consists of cells quite similar but considerably shorter. I am not able to distinguish any differences between the epidermal cells of different parts of the plant in this stage of its growth.

Origin of the secondary Hapteres.—Longitudinal sections through the stipe of a plant 12 cm. in length just above the primitive disc which has now increased in diameter to 5 mm., show the origin of the first secondary hapteres. I am not able to make a distinction between a rhizogenous area of the stipe and the rest of that organ, for as has been previously said, callosities which I consider equivalent to secondary hapteres may, under favorable conditions, be produced all the way up the stipe to the pneumatocyst. Those hemispherical emergences of the cortex which are produced close to the primitive disc develop as hapteric branches. The first appearance of the hapteres is as a slight swelling of the cortex and it will be found that this swelling is due to the more active divisions of a cambial layer lying between the central cylinder, now very distinct, and the epidermis. Soon this swelling becomes hemispherical and now the cells of its central portion are elongated in a direction parallel with the axis of the emergence. There is not any definite development of a central cylinder in the haptere, but the whole organ is made up of thin-walled somewhat prosenchymatous cells, covered with the characteristic epidermis, just below which the cells are short and flattened and in a state of rapid division concentrically with the surface of the emergence. In the hemispherical stage of the secondary haptere the central cells lying near the base of the emergence are many of them 150 mic. in length by 45 mic. in breadth, while the cambial cells three or four layers underneath the epidermis are 10 mic. in length and 15 mic. in breadth.

Dichotomy of the secondary Hapteres.—The primary hapteres do not commonly show dichotomy, but remain as crenations of the disc-margin. As the disc enlarges these crenations sometimes become indented and this indentation is equivalent to the sharp characteristic dichotomy of the secondary hapteres. In the latter after the first emergence has elongated into a cylinder with rounded end, the densely protoplasmic character of the apical region where the cambial cells, or meristem, is located, gives a darker appearance to the apex of the haptere. Gradually this apex becomes laterally compressed and an indentation appears at the summit separating two meristematic areas. Longitudinal sections through such apical areas show that the meristem of the exact apex ceases its active concentric divisions, while right and left of this region the divisions continue, thus forming two new apical cones, which continue to develop as before. Forking of the haptere originating in this manner may be repeated a number of times, and thus the much-branched later hapteres of the plant are developed. The cambial zone of the apex extends down the sides of the hapteric branch and is utilized in the progressive thickening of the organ. The haptere may then be regarded as a conic-cylindrical organ surrounded by an epidermal layer concentrically underneath which is a general cambial zone. By the division of the apical region of this zone the haptere increases in length; by longitudinal divisions in the lateral portions of the zone the haptere increases in thickness. Even in the most mature hapteric branches the lateral cambium is still visible as such and I have not been able to discover that the growth in thickness is definitely terminated except by the cold of the autumn, when the growth of the whole plant ceases and later the individual perishes.

Fixation of the Haptere.—If the end of an hapteric branch comes in contact with the surface of a rock or other object which gives the necessary resistance, a fixation-area is developed. The epidermal cells of the tip lose their chromatophores and the layers just within remain small but thicken their walls. The general shape of the cell-cavities throughout the fixation-area remains very similar to that of the cambial cells from which they were developed. Growth in length is now terminated, but growth in thickness continues. Sometimes one haptere affixes itself to a neighboring haptere, in which case the ordinary fixation-area arises precisely as if the organ had been affixed to a rock, but this obviously cannot be a common occurrence ; yet in every holdfast that is fully developed several such fixations of one haptere to another are likely to be met with.

Callosities of the Stipe.—The characteristic verrucose confluent or elongated callosities of the stipe originate from emergences precisely similar to those which in the holdfast region produce the hapteric branches. I have not observed dichotomy in these callosities, nor do their surfaces become modified into definite fixation-areas. Where two long stipes of adjacent plants have become entwined as frequently happens, the callosities are well developed all along the area of contact. Their structure is altogether equivalent to that of the hapteric branches, and as previously noted, I consider them homologous with hapteres. They may be regarded as cushions to prevent abrasion when two or more stipes have become intertwined.

Structure of the mature Haptere.—When full-grown the haptere consists of but four readily distinguishable tissue areas, the epidermis, the lateral cambium, the rather thick-walled fundamental tissue, and the fixation-area. Chromatophores are not so abundant nor deeply stained in the epidermis as in the same layer of the pneumatocyst or laminae, hence the hapteric region is of a much lighter green than the portions of the plant exposed to stronger illumination. The same is true of the epidermal region on the lower portion of the stipe. The cambial area in the mature haptere is still definitely differentiated as such and consists of the characteristic flattened cells with thinner walls than those of the fundamental tissue. The central fundamental tissue making up the great bulk of the organ is composed of rather thick-walled approximately isodiametrical parenchyma. The fixation-area consists of much smaller thick-walled cells shaped like those of the cambium.

Structure of Stipe.—In a young plant 18 mm. in length the stipe was .25 mm. in diameter midway between the primitive disc and the laminar expansion. Cross sections and vertical sections showed a central cylinder .08 mm. in diameter already sharply differentiated. It could be recognized in cross section by the smaller diameter of the cells and in longitudinal section by the greater comparative length. All the cells, however, within the clearly marked epidermal layer could be described as thin-walled parenchyma or prosenchyma. In material of this age mucilage-ducts were not seen, nor had the intercellular spaces of the pith-web begun to originate. The whole stipe was solid and approximately homogeneous. The cells throughout were strongly stained and many of the nuclei showed sharp and distinct mitotic figures.

In slightly older material than that just described the first intercellular spaces begin to appear as clefts between the lateral walls of the central pith cells, and a little later the layer of cells immediately surrounding the primitive pith develops the first sieve tubes, while at the same time the cortex rapidly increases in thickness. In a plant 12 cm. in length the stipe was 1 mm. in diameter and the central cylinder measured .25 mm. across. In this stage the pith-web made up of loose, anastomosing, branching, septate filaments is well established. The filaments of the pith-web at this time measured about 10 mic. in diameter. Between the meshes of the loose network an abundance of slime was present. At the periphery of the pith-web lay the "sieve-tubes," as they have been termed, the development of which from ordinary cortical cells was not difficult to follow. Most of the centrally disposed sieve-tubes appeared very much smaller and thicker walled in the cross section than did the peripheral elements. This was due to the longitudinal stretching of the inner and older tubes. In most of the cross sections through this material the sieve-tubes stood in radiating lines of three or four to each group. Although the trumpet-hyphae, reserving this term for the sieve-tube-like elements of the pith-web in contradistinction to those developed from the cortex, were not yet apparent in my 12 cm. material there were some perforated transverse walls visible in the ordinary anastomosing filaments of the web. Although my stains have not been nuclear some excellent mitotic figures were visible in this preparation.

Longitudinal sections through the 12 cm. material show the cortex to consist in general of thin-walled parenchymatous tissue made up of cells about twice as long as broad in the layers close to the epidermis but becoming progressively longer and slenderer towards the central cylinder, until those cells bounding the pith-web become transformed into the sieve-tubes. The pith-web cells are attached to the sieve-tube cells and to the undifferentiated layers just outside of the sieve-tube zone. The young sieve-tube is indistinguishable from an ordinary prosenchymatous cell of the inner cortex. The nuclei of some inner cortex cells undergo fragmentation and then these cells are greatly elongated as the stipe grows in length. As one elongates it becomes much narrower, so that while the diameter of the cell from which a sieve-tube originates may be 12 mic. and the length 80 mic. the diameter of the sieve-tube which arises from it may in its thinnest portion be scarcely more than 1 mic. while the length may exceed a millimeter! Cross sections through the slenderest part of such a sieve-tube show its wall to be thickened like a thermometer tube, while the cell contents, deeply stainable with aniline blue, fill the extremely delicate capillary cavity.

Observation of a series of longitudinal sections makes it seem probable that the first sieve-tubes formed, and many of the successive tubes, are elongated to such tenuity that they finally pull apart in the middle and then the free ends of the tube deliquesce into the common gelatinous slime of the pith-web leaving only the thickened so-called callus patches attached to the remnants of the tube and even these may disappear. The centrifugal production of sieve-tubes continues vigorously while the stipe is young, but in old material not so large a number proportionately are to be found. The stretching of the sieve-tube has all the appearance of a passive extension of the cell, while cross partitions are still being formed in the cortical region outside of the sieve-tube area. I believe that the fragmentation of the nucleus preventing the regular development of cross partitions in the mother-cell of the sieve-tube is the occasion of its failure to divide further and of its consequent passive elongation.

It was in this 12 cm. material that the best examples of cryptostomata were discovered. I shall return to their discussion later while considering the lamina. It suffices to mention at this point that these peculiar piliferous organs of doubtful morphological significance are present upon young stipe as well as upon young lamina, but in mature plants I have not seen them.

Origin of the Pneumatocyst.—A continuous ribbon of 3 mic. sections was taken across the area of the pneumatocyst. The series begins in definite stipe area, traverses the pneumatocyst and ends in the base of the lamina. The plant measured 12 cm. in length. In the undoubted stipe area the pith-web is seen to have its meshes filled with gelatine and the first appearance of the pneumatocyst is a small rift in the jelly near the center of the pith-web. As the series passes over through the pneumatocyst this first rift is seen to increase in size and others appear near it. At the same time a distinct flattening of the stipe takes place and it is worth noting that the primitive pneumatocyst is clearly elliptical in cross section rather than spherical. As the series continues across the pneumatocyst area rifts in the jelly of the pith network become smaller. The flattening of the whole area becomes more marked and in the base of the lamina the section has become five or six times as long as it is broad and shows the undoubted lamina characters. The pneumatocyst, stipe and lamina are essentially the same in structure, but the bubble which forms in the pith-web of the pneumatocyst area increases very rapidly in size and the vesicle thus formed becomes finally the greater retort-shaped organ of the mature plant.

Structure of older Stipes.—As the plant increases in size the stipe continues to thicken by concentric walls which appear in several of the sub-epidermal layers of the cortex. A plant 12 dm. in length showed a stipe 5 mm. in diameter of which the central cylinder occupied 1.5 mm. In material of this age the cortical cells have not yet developed the characteristically thick walls of mature stages, but mucilage canals are now in evidence, a circle of them appearing subepidermally. I am able to confirm Will's and Guignard's account of their development. They originate by vertical radial partitions of certain cortical cells in the cambium region. Just outside of the two cells thus formed a cleft appears and this cleft increases in size while the two small cells within divide by other vertical and transverse partitions finally coming to line the half of the canal which faces the central cylinder. These small cells are the secretion-cells. They do not persist but after a time break down so that in mature portions of the stipe the mucilage-duct in cross section appears merely as a circular-outlined intercellular space.

It is in material of the same age or younger that one finds well-developed trumpet-hyphae intermingled with the ordinary anastomosing filaments of the pith-web. While these cells do not become nearly so attenuated as the sieve-tubes, they are nevertheless slenderer and three or four times as long as the ordinary cells of the pith-web. Their ends, where two come in contact, are much swollen. I have not been able to discover whether fragmentation of the nucleus precedes the formation of a trumpet-hypha as it does that of the sieve-tube. Neither my Russow's callus reagent nor corallin-soda gave results such as those which Oliver obtained, nor have I been able by microchemical methods to demonstrate the presence of true callus, such as has been announced for the sieve-tubes. This is possibly owing to the preservatives which have been applied to the tissues, or their age, but I am inclined to accept rather the views of Wille regarding the callus than those of Oliver. No evidence of protoplasmic connections between adjacent sieve-tubes or trumpet-hyphae has been obtained. At this point it is well to state definitely that the material I have examined seems to show clearly that there are two very different kinds of tubular cells with perforated end partitions. Wille, in criticising the results of Oliver, who made a distinction between trumpet-hyphae and sieve-tubes, seems to suggest that there is only one category of such cells and that differences are of degree and not of kind. According to my observations the trumpet-hypha does not become extremely attenuated nor does it develop the thermometer-tube cell with capillary lumen such as characterizes the sieve-tube. Since the morphological position of the two kinds of cells in the stipe is different, since their origin is different, and on account of their very easily distinguishable structure, I can but follow Oliver and maintain them as separate structural elements not to be confused on account of their similar perforated end-plates. They are abundant in older material but the relative proportion of the two varieties of cells changes. While in young material an abundance of sieve-tubes is characteristic, in old material the trumpet-hyphae are abundant and but few sieve-tubes remain, most of them having undergone extreme attenuation and subsequent degeneration.

Structure of mature Stipe.—Cross sections through the stipe of a plant 25 meters in length showed its diameter to be 10 mm., of which the central cylinder comprised 2.5 mm. In this material the cambium zone lying four or five layers within the epidermis is still distinct. Numerous mucilage canals are present, most of them lying in the concentric circle first developed and now separated from the periphery of the stipe by numerous layers of cortex developed after their formation from the cambium. The average size of cortical cells in cross section is about 25 mic. Their walls, however, are now distinctly thicker than at first and at the angles between the cells the thickening is sometimes increased giving to the tissue a collenchymatous appearance. By the thickening of the walls great elasticity and strength is given to the stipe. Intermingled with the large cortical cells are many smaller ones averaging 10 mic. in diameter. The central cylinder in the mature stipe consists of a loose pith-web of anastomosing filaments, imbedded in gelatine, among which abundant large trumpet-hyphae are apparent. Many of the trumpet-hyphae connect by lateral processes with the ordinary filaments which are not more than half as great in diameter. In material of this age the sieve-tubes are very difficult to find, almost all of them having been destroyed. This is not what Oliver means by his phrase "obliteration of sieve-tubes" for he applied that term to the closing of the plates by his callus-like substance, nor can I learn that the fact has previously been recorded. Oliver mentions that the true sieve-tubes are abundantly branched. In my opinion this is a mistake. Anastomoses occur between sieve-tubes and the formative layer of the cortex from which they arise, but I have seen no true anastomoses between the sieve-tubes and the hyphae of the pith-web, nor have I observed any branching of the sieve-tubes by the formation of lateral emergences such as are so common in the trumpet-hyphae. The great abundance of the trumpet-hyphae and their peripheral position, as well as central, in the pith-web may easily have given rise to a misconception.

Structure of the Pneumatocyst Wall.—Sections of a pneumatocyst wall taken from a plant 12 dm. in length in which the pneumatocyst was approximately spherical and 4 cm. in diameter showed the wall of the cyst to be 4.5 mm. thick. The epidermis is not essentially different from other epidermal tissue and in the subepidermal regions a cambial layer is present by divisions of which the wall is thickened. The older cortical cells throughout the pneumatocyst wall have their long diameters parallel with the radii of the organ, until an inner cambial zone is reached close to the cavity of the cyst. Here the cells become tabellar in form with their long axes parallel with the surface. The pith-web is altogether destroyed, but in this material characteristic elongated sieve tubes with narrow lumina are present. The presence of such an inner cambial zone seems to be peculiar to the pneumatocyst area and in this zone numerous transverse as well as concentric walls are constantly being formed. The intermediate area between the inner and outer cambium, as the pneumatocyst matures into the retort-shaped body, finally comes to consist of cells elongated in the axis of growth rather than as at first perpendicular to this axis.

Structure of the young Lamina.—The basal structure of the lamina is identical with that of the stipe. Like the latter it must be considered to consist of central cylinder—in this case a very thin plate of cells—of cortex and of epidermis. My serial sections through stipe, pneumatocyst and young lamina show the progressive change from the cylindrical through the oval and elongated-oval to the thin ribbon-shaped section and enable the homologies of the various areas of the lamina and stipe to be exactly determined. Cross sections through the lamina of a plant 18 mm. in height showed the thickness of the lamina to be a little over .1 mm. while from edge to edge the lamina measured 4 mm. The most marked difference between young lamina and stipe is the early development in the former of mucilage canals which lie in rows just within the epidermis. The cortex in this stage consists of about two layers of cells, those just under the epidermis being generally larger than the ones which abut upon the plate of cells regarded here as central cylinder. The secretion cells of mucilage ducts in this material seem to line the canal not only along the inner side but along the outer as well. They stain deeply with aniline-water-safranin. The cells of the central plate are narrow, much thicker-walled than those of the pith-web in the stipe and packed together in such a way as to leave only very small intercellular spaces. Many of them run crosswise of the leaf while others run lengthwise. The result of this is to make this area not dissimilar to the same area in longitudinal section, but as the leaf matures the pith-web character of the middle lamella becomes more marked and trumpet-hyphae are present in longitudinal sections of the lamina of a 12 cm. plant. In a leaf of this size the cortex consists of five or six layers of cells, the inner larger than the outer, but along the middle lamella the cortical cells are smaller and elongated in the axis of the leaf. Where they abut on the middle lamella they pass over into the character of pith-web tissue. By the time the leaf has acquired this size the secretion-cells of the mucilage ducts have for the most part broken down and cryptostomata have developed in the furrows which lay over the mucilage ducts of the younger leaf. The epidermal cells in young leaves are about three times as broad as they are high, are densely protoplasmic and stain vividly. Interesting rows of short cylindrical cells are found in the pith-web, their diameter sometimes exceeding their height. Such cells finally become elongated into the ordinary hyphae of the web. Cross sections of the leaf of a 12 centimeter plant show some sieve-tubes still present and more abundant in the growing region of the leaf which is essentially basal.

Towards the tip of the leaf the lamina is thinner in the 12 cm. material, the epidermal cells are more nearly square in outline, the cortical cells are very large and approximately isodiametrical, while the central lamella is reduced to about two layers of thick-walled cells of elongated shape with few intercellular spaces. From this region mucilage ducts and sieve-tubes are absent for it was formed before the time of their differentiation, nor are cryptostomata abundant toward the tip of the leaf.

Splitting of the Lamina.—From a series of sections taken through young laminae of a plant in which the first cleft is beginning to appear I have been able to determine the origin and occasion of the cleft. In *Nereocystis* the cleft does not appear to be of the nature of a wound as said by Professor Setchell of the similar phenomenon in *Saccorhiza dermatodea,* but it seems to take place in this way: A single row of cortical cells immediately below the epidermis deliquesces or collapses and the epidermis furrows along the depression. The deliquescence is propagated to adjacent cells right and left of the furrow and continues down to the middle lamella. This furrowing may take place along one surface of the leaf or along both surfaces until the epidermal cells come to lie against the middle lamella. The latter then breaks down and the two epidermises at the bases of the furrows are contiguous. The split takes place along the base of the furrow and leaves the two halves of the lamina with apparently normal unwounded edges. In some cases the cortex cells come down together over the edge of the deliquescing central lamina so that it is extremely difficult to distinguish between the original edge of the lamina and the edge of the cleft. The epidermis suffers no disintegration during the process. The actual cleavage of the lamina may be due, as Professor Setchell suggests for *Saccorhiza,* purely to the impact of the waves upon the weakened structure, but it may also be due to a definite separation of the epidermal cells from each other by a chemical change in their walls. The furrow of the epidermis seems to deepen, destroying the inner cells of the lamina as it progresses. The split takes place first in the more complex basal portion of the leaf and is perpetuated to the tip. I have not been able to determine whether the cleft is propagated in this manner clear to the simpler primitive-tip end of the leaf, or whether it becomes a mechanical cleft of the nature of a wound when it reaches the distal end of the lamina.

No evidence has been secured to indicate that there is any renovation of the lamina in *Nereocystis* such as is well known to take place in some of the Laminariaceae.

Structure of the Cryptostomata.—The organs of the young stipe and lamina which are with some hesitation termed cryptostomata appear as short, irregular furrows from the surface of which tufts of two- or three-celled hairs are produced. They are not so conspicuous in *Nereocystis* material that I have examined as those of *Adenocystis*, *Alaria* and *Saccorhiza* described by Kjellman and Murray. I have failed to find them save on young plants less than half a meter in height. Various suggestions have been made by different students of the Phaeophyceae regarding their significance. By some they are regarded as vestigial reproductive tracts, but it will be unnecessary to go into this further than to make the suggestion that the areas classed as cryptostomata in different genera of brown algae are not by any means necessarily to be considered as everywhere the same. Indeed it is quite clear that in the Splachnidiaceae and Laminariaceae they are probably of different significance from those of Fucaceae. They stain deeply with aniline dyes in *Nereocystis* and I suspect from this fact that I have not seen mature stages of the hairs. There is a possibility that the mucilage canals are invaginated furrows and that the so-called cryptostomata are developmental stages of these, but I have not satisfied myself upon this point.

Primitive Furrows of the Lamina.—An interesting character which is to be noted in very young plants is a longitudinal furrowing of the lamina by parallel grooves which occur on both sides, each groove lying over a mucilage canal. In the primitive tip where mucilage canals are absent the furrows also are absent and leaves two or three centimeters in length have lost these furrows as may be seen in cross section, but in plants 1–2 cm. in height a deep furrow lies over each longitudinal mucilage canal just within the epidermis. Something of an appearance similar to that of young *Costaria* plants is given by these longitudinal furrows. But in *Costaria* the striation of the lamina arises, as shown by cross sections, from ridges which structurally belong to the cortex and over which the epidermis is elevated by the growth of inner portions of the lamina. Nor in *Costaria* do the ridges bear the same relation to mucilage ducts that is borne by the primitive furrows in the *Nereocystis* sporeling. Indeed I have not observed mucilage ducts in young *Costaria* laminae.

Origin of Secretion-cells in the Lamina.—It has already been noted that the secretion-cells seem to line all sides of the mucilage duct in young lamina while in young stipe they occur only on the side of the duct which is toward the central cylinder. The occasion for this seems to be explained by some of my sections which show the first division-wall of the primitive secretion-cell parallel with the face of the lamina instead of perpendicular to the surface as in the stipe. The cleft then arises between these two small cells, one lying peripherally and one centrally. But in the stipe the first cleft appears in a plane perpendicular to the surface and not between the two primitive secretion-cells, but between the cells just peripheral to them. I do not like to speak with positiveness upon this point since it is at variance with the results of previous investigations upon other genera, and but a few of my sections are helpful.

Growth of the Lamina in Length and Thickness.—As in other Laminariaceae each lamina of *Nereocystis* grows by a generally basal area which lengthens in both directions, so that the elongation of the lamina is neither strictly basipetal or acropetal. The thickening of the lamina, which finally, in old leaves, comes to consist of from five to ten cortical layers on each side of the central lamella which is itself made up of a rather compact pith-web tissue eight or more layers across, goes on in the general basal area of growth. Old laminae are of a mature type of structure from base to tip since the original thinner primitive tip area has been worn away by the action of the waves and the disappearance of the primitive tip is often to be noted even in very young plants less than 12 cm. in length.

Origin of the Sorus.—The sorus of *Nereocystis* in its structure and origin is altogether typical of the family. The first evidence of the sorus is marked by transverse divisions in the epidermal cells parallel to the surface of the lamina. In this way a double layer of somewhat larger deeper-stained superficial cells and smaller cubical more dimly-stained sub-epidermal cells comes into existence. The superficial cells elongate into the club-shaped paraphyses which finally come to be 30–40 mic. in length, about 7 mic. in diameter at the capitate tip and 2 mic. or even less where they join the basal cells. The sporangium originates as an hemispherical bud on the basal cell beside the paraphysis. By the attenuation of the paraphyses as they elongate space is afforded the sporangia for their development. In half-mature sori in which the paraphyses were 20 mic. in height the sporangia could be seen as ellipsoid cells about half as long and of quite different shape from the already club-shaped paraphyseal cells. In mature sori, however, when the spores have been formed in the sporangia the difference in the height of the two cells is not so great and the paraphyses overtop the sporangia by but about 10 mic. or even less. The distal end wall of the paraphyses is thickened as in other genera of the same subdivision of the family.

Free zoöspores have not been seen but sporangia ready to open have been found and the spores appear as hyaline cells close to 1 mic. in the short diameter and a very little longer transverse to this. The sporangia doubtless open at the tip to discharge the hundred or more spores contained in each. The end wall of the sporangium, like that of the paraphysis is often considerably thickened. I am able to confirm upon *Nereocystis* material the results of Thuret who noted in 1850 the separation of a thin cuticular pellicle from the surface of sori in *Scytosiphon*, *Laminaria* and some Fucaceae. This pellicle retains the partition-markings of the original epidermal cells quite as figured by Thuret for *Laminaria saccharina* and *Scytosiphon lomentarius*. The exact manner in which this pellicle is separated does not yet appear to be clearly understood, nor am I able to say more about it at this time than that the wall of the soral surface when young seems to be lamellose and the separation of the cuticular pellicle seems to take place by the dissolving of one of the lamellae. Before the separation a few very small bodies, red-stained in aniline-safranin preparations are seen lying against the inner face of the distal wall of each paraphysis. It is possible that they assist in the secretion of the thick pellicle which is finally sloughed off. Sometimes two transverse divisions precede the formation of the paraphysis in which case two layers of floor-cells are produced in the sorus. One or two jointed paraphyses have been seen. The paraphysis seems never to consist of more than two cells and the two-celled condition is extremely rare.

I am under obligation to Miss Josephine E. Tilden for putting at my disposal an abundance of carefully preserved material and to Mr. Harold Lyon for assistance in the tedious routine of microtomy. The drawings were made by Miss Tilden under my direction.

Explanation of Plates.

PLATE 361

FIG. 1. Plant .1 mm. in length. Shows primary differentiation of holdfast and stipe-laminar region. Enlarged.

FIG. 2. Plant 1 mm. in length. Stipe is already elongated. Tip of lamina is removed. Enlarged.

FIG. 3. Three young plants, each one-half natural size. The smallest was 6 mm. in length, the next 18 mm. and the largest 4.5 cm. These plants show the early rapid enlargement of the laminar area.

FIG. 4. A plant 14 cm. in length, reduced one-half, showing the origin of the first cleft near the base. The stipe is proportionally undergoing more rapid elongation in this stage

FIG. 5. Pneumatocyst and laminar bases from a plant 50 cm. in length. Reduced one-half. Showing how only the first cleft reaches the surface of the pneumatocyst.

FIG. 6. Vertical section of primary fixation-area, showing rhizoid cells. From plant 18 mm. long. × 335.

FIG. 7. Diagrammatic cross section of stipe. Sieve-tubes represented as dots. Plant 12 cm. in length. × 25.

FIG. 8. Diagrammatic cross section through pneumatocyst of plant 12 cm. in length. Black spaces in central cylinder represent clefts in the gelatinous matrix. × 25.

FIG. 9. Diagrammatic cross section through base of primary lamina. Plant 12 cm. in length. × 25.

FIG. 10. Cross section through pneumatocyst of 12 cm. plant. Peripheral region. × 335.

FIG. 11. Cross-section through pneumatocyst of 12 cm. plant. Sieve-tube region. × 335.

FIG. 12. Diagrammatic cross section of lamina in 18 mm. plant. Mucilage ducts and grooves are indicated × 25.

FIG. 13. Detail of laminar structure. Cross-section 25 mm. above the top of the pneumatocyst in 12 cm. plant. × 335.

PLATE 362

FIG. 14. Cross section through base of lamina in 12 cm. plant showing groove which initiates the longitudinal division of the laminae. 25 mm. above top of pneumatocyst. × 335.

FIG. 15. Cryptostomatal area. Cross section immediately above pneumatocyst of plant 12 cm. in length.

FIG. 16. Sieve-tube from stipe. 12 cm. plant. Shows the fragmented nuclei in the capillary cavity of the cell. × 335.

FIG. 17. Trumpet-hypha from pith-web of plant 12 dm. in length. Shows gelatinous thickening of inner wall. × 335.

FIG. 18. Origin of sieve-tubes. Longitudinal section through area bounding the pith-web. Plant 12 cm. long. Cells to the left with several nuclei become passively elongated into the sieve-tubes. × 335.

FIG. 19. Cross section of mucilage duct in the lamina. Section made immediately above pneumatocyst. Plant 12 cm. long. × 335. Should be compared with Fig. 15 and indicates a possible relation between the structures classed as cryptostomata and the mucilage ducts.

FIG. 20. Cross section of old mucilage duct in stipe. Plant 12 cm. long. Secretion-cells not shown. × 335.

FIG. 21. Cross section of pneumatocyst wall. Mucilage duct in center. × 335.

FIG. 22. Origin of paraphyses in sorus. Mature plant. × 335.

FIG. 23. Origin of sporangia in sorus. Mature plant. × 521.

FIG. 24. Cross section through mature sorus showing paraphyses and sporangia. In the latter spores are indicated. × 335.